

Romantic Love: An fMRI Study of a Neural Mechanism for Mate Choice

HELEN FISHER,^{1*} ARTHUR ARON,² AND LUCY L. BROWN³

¹Department of Anthropology, Rutgers University, New Brunswick, New Jersey 08901

²Department of Psychology, State University of New York at Stony Brook,
Stony Brook, New York 11794

³Departments of Neurology and Neuroscience, Albert Einstein College of Medicine,
Bronx, New York 10461

ABSTRACT

Scientists have described myriad traits in mammalian and avian species that evolved to attract mates. But the brain mechanisms by which conspecifics become attracted to these traits is largely unknown. Yet mammals and birds express mate preferences and make mate choices, and data suggest that this “attraction system” is associated with the dopaminergic reward system. It has been proposed that intense romantic love, a cross-cultural universal, is a developed form of this attraction system. To determine the neural mechanisms associated with romantic love we used functional magnetic resonance imaging (fMRI) and studied 17 people who were intensely “in love” (Aron et al. [2005] *J Neurophysiol* 94:327–337). Activation specific to the beloved occurred in the right ventral tegmental area and right caudate nucleus, dopamine-rich areas associated with mammalian reward and motivation. These and other results suggest that dopaminergic reward pathways contribute to the “general arousal” component of romantic love; romantic love is primarily a motivation system, rather than an emotion; this drive is distinct from the sex drive; romantic love changes across time; and romantic love shares biobehavioral similarities with mammalian attraction. We propose that this attraction mechanism evolved to enable individuals to focus their mating energy on specific others, thereby conserving energy and facilitating mate choice—a primary aspect of reproduction. Last, the corticostriate system, with its potential for combining diverse cortical information with reward signals, is an excellent anatomical substrate for the complex factors contributing to romantic love and mate choice. *J. Comp. Neurol.* 493:58–62, 2005.

© 2005 Wiley-Liss, Inc.

Indexing terms: romantic love; dopamine; fMRI; mate choice

Charles Darwin distinguished between two types of sexual selection: intrasexual selection, by which members of one sex evolve traits that enable them to compete directly with one another to win mating opportunities, and intersexual selection, by which individuals of one sex evolve traits that are *preferred* by members of the opposite sex, a process known as “mate choice” (Darwin, 1871). Scientists have described many physical and behavioral traits in birds and mammals that evolved by mate choice. The peacock’s tail feathers is the standard example. But no one had defined the corresponding neural mechanism by which the “display chooser” comes to prefer certain traits and focuses his/her mating energy on a *particular* conspecific, thereby making a mate choice. Yet it is well established that many creatures have mate preferences, focus their courtship energy on these specific individuals, and make mate choices. In fact, the phenomenon of mate

choice is so common in nature that the ethological literature regularly uses several terms to describe it, including “mate choice,” “female choice,” “mate preference,” “individual preference,” “favoritism,” “sexual choice,” and “selective proceptivity” (Andersson, 1994).

Fisher (Fisher, 1998; Fisher et al., 2002a) hypothesized that mate choice is associated with a specific brain system for “courtship attraction” that operates in tandem with other neural systems, including the circuits for the sex

*Correspondence to: Helen Fisher, Department of Anthropology, Rutgers University, New Brunswick, NJ 08901.

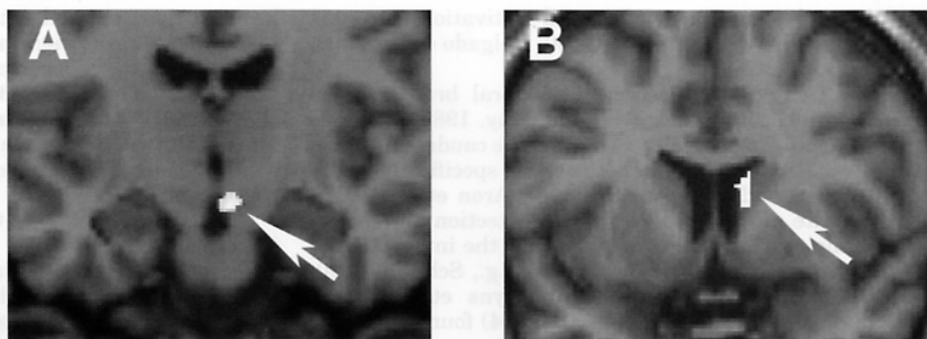
E-mail: helenfisher@helenfisher.com

Received 30 March 2005; Revised 24 June 2005; Accepted 5 August 2005

DOI 10.1002/cne.20772

Published online in Wiley InterScience (www.interscience.wiley.com).

Fig. 1. Group activation regions detected as individuals looked at an image of their beloved compared to an image of an acquaintance (see Aron et al., 2005, for details). The regions of activation (white) are from anatomically normalized data and are superimposed on a template brain from SPM99. **A:** The right ventral tegmental area (arrow) was activated. **B:** The right caudate nucleus (arrow) was activated. Data from other studies of mammals suggest that these regions are involved in reward and motivation functions.



drive, sensory perception, discrimination, and memory; courtship attraction is expressed at different times and to different degrees in different species according to each species' specific reproductive strategy; and this neural network evolved to enable "display choosers" to focus their mating energy on specific, potential mating partners, thereby conserving courtship time and metabolic energy. In most mammalian and avian species this attraction is brief, lasting only minutes, hours, days, or weeks. In humans the neural mechanism associated with courtship attraction is developed, forming the physiological basis of what is commonly known as passionate love, obsessive love, "being in love," or romantic love.

We chose to study courtship attraction in humans by looking at early stage intense romantic love for several reasons. Early stage, intense romantic love is regarded as a human universal or near universal experience (Jankowiak and Fischer, 1992); this neural system is associated with a specific constellation of identifiable motivations, emotions, and behaviors (Tennov, 1979; Hatfield and Sprecher, 1986; Shaver et al., 1987; Hatfield et al., 1988; Harris and Christenfeld, 1996; Fisher, 1998; Gonzaga et al., 2001) and these identifiable features are easily observed, quantified, and tabulated in humans. Some of these traits studied by the above-cited investigators include focused attention on the beloved, increased energy, elation, and mood swings. Often, the lover experiences a pounding heart, sweaty palms, and other sympathetic nervous system reactions while with the beloved and "separation anxiety" when apart. Lovers express emotional dependence; they change their habits to impress and/or remain in contact with the beloved. Adversity heightens romantic passion, known as "frustration attraction." Lovers exhibit extreme empathy toward the beloved; many are willing to die for this "special" individual. They also express sexual desire for him or her, as well as intense sexual possessiveness, yet the craving for emotional union supersedes the need for sexual contact. A central characteristic of human romantic love is intrusive, obsessive thinking about the beloved. Rejected lovers generally protest and try to win the beloved back, as well as express "abandonment rage" and despair. Romantic passion is also involuntary, difficult to control, and regularly impermanent.

We used functional magnetic resonance imaging (fMRI) methods to test two hypotheses about the neural mechanisms associated with romantic love (Aron et al., 2005). First, romantic love would involve subcortical dopaminergic pathways that mediate reward (Liebowitz, 1983;

Fisher, 1998). Second, romantic love would involve neural pathways associated with goal-directed behaviors, supporting the prediction that romantic love is a goal-directed state that leads to a range of emotions, rather than a specific emotion (Aron and Aron, 1991; Aron et al., 1995).

For details of the investigation, see Aron et al. (2005). Briefly, 10 women and seven men were recruited by word of mouth and with flyers seeking individuals who were currently intensely in love. The age range was 18–26 years ($M = 20.6$; median = 21), and the reported duration of "being in love" was 1–17 months ($M = 7.4$; median = 7). Each participant was orally interviewed in a semistructured format to establish the duration, intensity, and range of his or her feelings of romantic love. Each also completed the Passionate Love Scale (PLS), a 9-point Likert scale self-report questionnaire which measures several traits commonly associated with romantic love (Hatfield and Sprecher, 1986) (Cronbach's alpha for questionnaire reliability in this study = 0.81; Cronbach, 1951).

A preliminary investigation identified a photograph of the beloved as an effective stimulus for eliciting feelings of intense romantic love (Mashek et al., 2000). So our protocol employed photographs and consisted of four tasks presented in an alternating block design: For 30 seconds each participant viewed a photo of his/her beloved (positive stimulus); for the following 40 seconds each participant performed a countback distraction task; for the following 30 seconds each participant viewed a photograph of an emotionally neutral acquaintance (neutral stimulus); for the following 20 seconds each participant performed a similar countback task. The countback task involved viewing a large number, such as 8,421, and mentally counting backwards (beginning with this number) in increments of seven. We included the countback task to decrease the carryover effect after the participant viewed the positive stimulus because it is difficult to quell intense feelings of romantic love. This four-part sequence (or a counterbalanced version beginning with the neutral stimulus) was repeated six times; the total stimulus protocol was 720 seconds (12 minutes). Prescanning instructions were to think about a nonsexual, euphoric experience with the beloved; postscanning interviews established that the participants had engaged in romantic thinking and feeling.

Group activation specific to the beloved occurred in several regions, including the right ventral tegmental area (VTA), localized in the region of A10 dopamine cells (Aron et al., 2005) (Fig. 1). The VTA is a central part of the brain's "reward system" (Wise, 1996; Schultz, 2000; Martin-Soelch et al., 2001) associated with pleasure, gen-

eral arousal, focused attention, and motivation to pursue and acquire rewards (Schultz, 2000; Delgado et al., 2000; Elliot et al., 2003).

The VTA sends projections to several brain regions (Gerfen et al., 1987; Oades and Halliday, 1987; Williams and Goldman-Rakic, 1998), including the caudate nucleus, where we also found group activations, specifically in the right medial and posterodorsal body (Aron et al., 2005). The caudate plays a role in reward detection and expectation, the representation of goals, and the integration of sensory inputs to prepare for action (e.g., Schultz, 2000; Martin-Soelch et al., 2001; Lauwereyns et al., 2002; O'Doherty et al., 2002). Zald et al. (2004) found that predictable monetary reward presentation caused dopamine release in the medial caudate body where we found activation.

These data suggest that our hypotheses are correct: romantic love is associated with subcortical dopaminergic pathways in the reward system, and romantic love is primarily a motivation system, which leads to various emotions, rather than a specific emotion. However, activation of subcortical dopaminergic pathways of the VTA and caudate nucleus may comprise only the "general arousal" component (Pfaff, 1999) of early-stage intense romantic love.

Nevertheless, these data suggest two important things about romantic passion: Foremost, romantic love may be a *primary* motivation system, a fundamental human mating drive. Pfaff (1999) defines a drive as a neural state that energizes and directs behavior to acquire a particular biological need to survive or reproduce; and he reports that all drives are associated with the activity of dopamine. Like drives, romantic love is tenacious; it is focused on a specific reward; it is not associated with any particular facial expression; it is exceedingly difficult to control; and it is associated with dopamine-rich neural regions (Fisher, 2004). Drives lie along a continuum. Thirst is almost impossible to control, while the sex drive can be redirected, even quelled. Falling in love is evidently stronger than the sex drive because when one's sexual overtures are rejected, people do not kill themselves or someone else. Rejected lovers sometimes commit suicide or homicide.

These data also indicate that romantic love is distinct from the sex drive, as suggested earlier (Aron and Aron, 1991; Fisher, 1998), because fMRI studies of human sexual arousal show regional activation in largely different brain regions than those we saw for our participants (Redoute et al., 2000; Arnow et al., 2002).

Using fMRI, Bartels and Zeki (2000:3829) also investigated brain activity in 17 men and women who reported being "truly, deeply, and madly in love." But the participants in that study had been in love substantially longer than those in our study (28.8 months vs. 7.4 months t [32] = 4.28, $P < 0.001$). They were also less intensely in love. This was established because both study groups were (serendipitously) administered the same questionnaire on romantic love, the PLS (scores of 7.55 vs. 8.54, t [31] = 3.91, $P < 0.001$).

Bartels and Zeki (2000; 2004) found activity in regions of the ventral tegmental area and caudate nucleus, as we did. However, they also found activity in the anterior cingulate and mid-insular cortex, results which stimulated us to examine our subset of subjects in longer relationships (8–17 months), as compared to our shorter-term participants. Among these participants, several more

brain regions showed activity, including the right mid-insular cortex, the right anterior and posterior cingulate cortex, and the right posterior cingulate/retrosplenial cortex. Thus, we confirmed Bartels and Zeki's (2000) finding that these brain regions are involved in longer-term love relationships. In addition, these combined data suggest that the neural mechanism for mate choice is dynamic: it changes across time.

Our subjects in longer-term relationships also showed increased activity in the ventral pallidum. The ventral pallidum has been associated with attachment behaviors in prairie voles (Lim et al., 2004; Lim and Young, 2004). These data suggest that as romantic love changes across time, brain systems associated with attachment increase activity—perhaps to enhance relationship stability and motivate parenting behaviors.

It has been proposed (Fisher, 1998; Fisher et al., 2002b) that mammalian and avian species evolved three distinct, dynamic, interrelated brain systems for courtship, mating, and parenting: The sex drive evolved to motivate individuals to seek a range of mating partners; courtship attraction (and its developed form, human romantic love) evolved to motivate individuals to focus their mating energy on specific partners, thereby conserving mating time and energy; and attachment evolved to motivate mates to remain together long enough to complete species-specific parental duties. These data may suggest one of the neural mechanisms by which this transition from attraction to attachment occurs.

As discussed above, it is well established that birds and mammals have mate preferences and make mate choices. This attraction is regularly associated with heightened energy, focused attention, obsessive following, sleeplessness, loss of appetite, possessive "mate guarding," affiliative gestures, goal-oriented courtship behaviors, and intense motivation to win a specific mating partner (Fisher, 2004), traits also associated with human early-stage, intense romantic love. Moreover, animal studies indicate that elevated activity of central dopaminergic neurons may play a primary role in mammalian mate preference (Fabre-Nys, 1998; Wang et al., 1999; Gingrich et al., 2000). When a female prairie vole is mated with a male, she forms a distinct preference for this partner, and when a dopamine agonist is infused into the nucleus accumbens she begins to prefer a male present at the time of infusion, even if she has not mated with this male (Gingrich et al., 2000; Liu and Wang, 2003). Also, electrochemical studies in male rats have shown increased dopamine release in the dorsal and ventral striatum in response to the presence of a receptive female rat (Robinson et al., 2002; Montague et al., 2004).

Thus, evidence from human fMRI studies support the hypothesis that multiple reward regions using dopamine are activated during feelings of romantic love, and this human phenomenon shows behavioral and neural system similarities with other mammalian species. The human form of courtship attraction, romantic love, may have begun to develop by 3.5 million years BP, because recent analysis of sexual dimorphisms in *Australopithecus africanus* suggests that early hominids were "principally monogamous" by this time (Reno et al., 2003).

Our fMRI results also suggest something about integrative events in the brain that lead to complex behavior and emotion. For example, we conducted a between-subjects analysis correlating degree of the BOLD response with

subjects' scores on the PLS. While viewing their beloved, those who self-reported higher levels of romantic love also showed greater activation in the right anteromedial caudate body ($r = 0.60$; $P = 0.012$). This result provides strong evidence for the link between a specific brain region and a specific brain function, romantic love. However, this specific region was also activated during anticipation of a monetary reward (Knutson et al., 2001), during reward-based stochastic learning (Haruno et al., 2004), and during attention tasks (Zink et al., 2003). Thus, this area of the anteromedial body of the caudate may be specifically associated with the rewarding, visual, and attentional aspects of romantic love. Because the caudate nucleus has widespread afferents from all of the cortex except V1 (Kemp and Powell, 1970; Selemon and Goldman-Rakic, 1985; Saint-Cyr et al., 1990; Eblen and Graybiel, 1995; Flaherty and Graybiel, 1995) and is organized to integrate diverse sensory, motor, and limbic functions (Brown, 1992; Parent and Hazrati, 1995; Brown et al., 1998; Haber, 2003), caudate nucleus anatomy is an appropriate mechanism for integrating the various aspects of this multifactor physiological and behavioral state, romantic love.

The range and variation of motivations and emotions associated with human romantic love are undoubtedly produced by many neural systems, acting in parallel and dynamic combinations. Nevertheless, several results support our hypotheses that early-stage, intense romantic love is importantly influenced by subcortical reward regions that are dopamine-rich (Fisher, 1998); that romantic love is primarily a neural system associated with motivation to acquire a reward, rather than a specific emotion (Aron and Aron, 1991); that this brain system is distinct, yet overlapping with the sex drive; that this brain system is derived from mammalian precursors (Fisher, 2004); and that it evolved as a mechanism to enable individuals to respond to sexually selected courtship traits and motivate individuals to make a mate choice (Fisher et al., 2002a).

In a study of 37 societies, Buss (1994) reports that men and women rank love, or mutual attraction, as the first criterion for choosing a spouse. This brain system has inspired love songs, love poems, love magic, myths and legends about love, and suicide and homicide cross-culturally (Jankowiak and Fischer, 1992; Fisher, 2004). Romantic love is most likely a primary aspect of our complex human reproductive strategy.

LITERATURE CITED

- Andersson M. 1994. Sexual selection. Princeton, NJ: Princeton University Press.
- Arnow BA, Desmond JE, Banner LL, Glover GH, Solomon A, Polan ML, Lue TF, Atlas SW. 2002. Brain activation and sexual arousal in healthy, heterosexual males. *Brain* 125:1014–1023.
- Aron A, Aron EN. 1991. Love and sexuality. In: McKinney K, Sprecher S, editors. *Sexuality in close relationships*. Hillsdale, NJ: Lawrence Erlbaum. p 25–48.
- Aron A, Paris M, Aron EN. 1995. Falling in love: prospective studies of self-concept change. *J Pers Social Psychol* 69:1102–1112.
- Aron A, Fisher H, Mashek D, Strong G, Li H, Brown LL. 2005. Reward, motivation and emotion systems associated with early-stage intense romantic love. *J Neurophysiol* 94:327–337.
- Bartels A, Zeki S. 2000. The neural basis of romantic love. *Neuroreport* 11:3829–3834.
- Bartels A, Zeki S. 2004. The neural correlates of maternal and romantic love. *Neuroimage* 21:1155–1166.
- Brown LL. 1992. Somatotopic organization in rat striatum: evidence for a combinatorial map. *Proc Natl Acad Sci U S A* 89:7403–7407.
- Brown LL, Smith DM, Goldbloom LM. 1998. Organizing principles of cortical integration in the rat neostriatum: corticostriate map of the body surface is an ordered lattice of curved laminae and radial points. *J Comp Neurol* 392:468–488.
- Buss DM and 49 colleagues. 1990. International preferences in selecting mates: a study of 37 cultures. *J Cross-cult Psychol* 21:5–47.
- Cronbach LJ. 1951. Coefficient alpha and the internal structure of tests. *Psychometrika* 16:297–334.
- Darwin C. 1871. *The descent of man and selection in relation to sex*. New York: Modern Library/Random House.
- Delgado MR, Nystrom LE, Fissel C, Noll DC, Fiez JA. 2000. Tracking the hemodynamic responses to reward and punishment in the striatum. *J Neurophysiol* 84:3072–3077.
- Eblen F, Graybiel AM. 1995. Highly restricted origin of prefrontal cortical inputs to striosomes in the macaque monkey. *J Neurosci* 15:5999–6013.
- Elliott R, Newman JL, Longe OA, Deakin JFW. 2003. Differential response patterns in the striatum and orbitofrontal cortex to financial reward in humans: a parametric functional magnetic resonance imaging study. *J Neurosci* 23:303–307.
- Fabre-Nys C. 1998. Steroid control of monoamines in relation to sexual behaviour. *Rev Reprod* 3:31–41.
- Fisher H. 1998. Lust, attraction, and attachment in mammalian reproduction. *Hum Nat* 9:23–52.
- Fisher H. 2004. *Why we love: the nature and chemistry of romantic love*. New York: Henry Holt.
- Fisher H, Aron A, Mashek D, Li H, Strong G, Brown LL. 2002a. The neural mechanisms of mate choice: a hypothesis. *Neuroendocrinol Lett* 23(Suppl 4):92–97.
- Fisher H, Aron A, Mashek D, Strong G, Li H, Brown LL. 2002b. Defining the brain systems of lust, romantic attraction and attachment. *Arch Sex Behav* 31:413–419.
- Flaherty AW, Graybiel AM. 1995. Motor and somatosensory corticostriatal projection magnifications in the squirrel monkey. *J Neurophysiol* 74:2638–2648.
- Gerfen CR, Herkenham M, Thibault J. 1987. The neostriatal mosaic. II. Patch- and matrix-directed mesostriatal dopaminergic and non-dopaminergic systems. *J Neurosci* 7:3915–3934.
- Gingrich B, Liu Y, Cascio C, Wang Z, Insel TR. 2000. D2 receptors in the nucleus accumbens are important for social attachment in female prairie voles (*Microtus ochrogaster*). *Behav Neurosci* 114:173–183.
- Gonzaga GC, Keltner D, Londahl EA, Smith MD. 2001. Love and the commitment problem in romantic relations and friendship. *J Pers Soc Psychol* 81:247–262.
- Haber SN. 2003. The primate basal ganglia: parallel and integrative networks. *J Chem Neuroanat* 26:317–330.
- Harris H. 1995. Rethinking heterosexual relationships in Polynesia: a case study of Mangaia, Cook Island. In: Jankowiak W, editor. *Romantic passion: a universal experience?* New York: Columbia University Press.
- Harris CR, Christenfeld N. 1996. Gender, jealousy, and reason. *Psychol Sci* 7:364–366.
- Haruno M, Kuroda T, Doya K, Toyama K, Kimura M, Samejima K, Imamizu H, Kawato M. 2004. A neural correlate of reward-based behavioral learning in caudate nucleus: a functional magnetic resonance imaging study of a stochastic decision task. *J Neurosci* 24:1660–1665.
- Hatfield E, Sprecher S. 1986. Measuring passionate love in intimate relationships. *J Adolesc* 9:383–410.
- Hatfield E, Schmitz E, Cornelius J, Rapson RL. 1988. Passionate love: how early does it begin? *J Psychol Hum Sex* 1:35–51.
- Jankowiak WR, Fischer EF. 1992. A cross-cultural perspective on romantic love. *Ethnology* 31:149.
- Kemp JM, Powell TP. 1970. The cortico-striate projection in the monkey. *Brain* 93:525–546.
- Knutson B, Adams CM, Fong GW, Hommer D. 2001. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *J Neurosci* 21:RC159.
- Lauwereyns J, Takikawa Y, Kawagoe R, Kobayashi S, Koizumi M, Coe B, Sakagami M, Hikosaka O. 2002. Feature-based anticipation of cues that predict reward in monkey caudate nucleus. *Neuron* 33:463–473.
- Liebowitz M. 1983. *The chemistry of love*. Boston: Little Brown.
- Lim MM, Young LJ. 2004. Vasopressin-dependent neural circuits under-

- lying pair bond formation in the monogamous prairie vole. *Neuroscience* 125:35–45.
- Lim MM, Wang Z, Olazabal DE, Ren X, Terwilliger EF, Young LJ. 2004. Enhanced partner preference in a promiscuous species by manipulating the expression of a single gene. *Nature* 429:754–757.
- Liu Y, Wang ZX. 2003. Nucleus accumbens oxytocin and dopamine interact to regulate pair bond formation in female prairie voles. *Neuroscience* 121:537–544.
- Martin-Soelch C, Leenders KL, Chevalley AF, Missimer J, Kunig, G, Magyar S, Mino A, Schultz W. 2001. Reward mechanisms in the brain and their role in dependence: evidence from neurophysiological and neuroimaging studies. *Brain Res Rev* 36:139–149.
- Mashek D, Aron A, Fisher HE. 2000. Identifying, evoking, and measuring intense feelings of romantic love. *Represent Res Soc Psychol* 24:48–55.
- Montague PR, McClure SM, Baldwin PR, Phillips PE, Budygin EA, Stuber GD, Kilpatrick MR, Wightman RM. 2004. Dynamic gain control of dopamine delivery in freely moving animals. *J Neurosci* 24:1754–1759.
- Oades RD, Halliday GM. 1987. Ventral tegmental (A10) system: neurobiology. 1. Anatomy and connectivity. *Brain Res* 434:117–165.
- O'Doherty JP, Deichmann R, Critchley HD, Dolan RJ. 2002. Neural responses during anticipation of a primary taste reward. *Neuron* 33:815–826.
- Parent A, Hazrati LN. 1995. Functional anatomy of the basal ganglia. I. The cortico-basal ganglia-thalamo-cortical loop. *Brain Res Brain Res Rev* 20:91–127.
- Pfaff DW. 1999. *DRIVE: neurobiological and molecular mechanisms of sexual motivation*. Cambridge, MA: MIT Press.
- Redoute J, Stoleru S, Gregoire MC, Costes N, Cinotti L, Lavenne F, Le Bars D, Forest MG, Pujol JF. 2000. Brain processing of visual sexual stimuli in human males. *Hum Brain Mapp* 11:162–177.
- Reno, PL, Meindl RS, McCollum MA, Lovejoy CO. 2003. Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. *Proc Natl Acad Sci U S A* 10:1073.
- Robinson DL, Heien ML, Wightman RM. 2002. Frequency of dopamine concentration transients increases in dorsal and ventral striatum of male rats during introduction of conspecifics. *J Neurosci* 22:10477–10486.
- Saint-Cyr JA, Ungerleider LG, Desimone R. 1990. Organization of visual cortical inputs to the striatum and subsequent outputs to the pallidum: nigral complex in the monkey. *J Comp Neurol* 298:129–156.
- Selemon LD, Goldman-Rakic PS. 1985. Longitudinal topography and interdigitation of corticostriatal projections in the rhesus monkey. *J Neurosci* 5:776–794.
- Schultz W. 2000. Multiple reward signals in the brain. *Nat Rev Neurosci* 1:199–207.
- Shaver P, Schwartz J, Kirson D, O'Connor C. 1987. Emotion knowledge: further exploration of a prototype approach. *J Pers Soc Psychol* 52:1061–1086.
- Tennov D. 1979. *Love and limerence: the experience of being in love*. New York: Stein and Day.
- Wang, Z, Yu, G, Cascio, C, Liu, Y, Gingrich, B, Insel TR. 1999. Dopamine D2 receptor-mediated regulation of partner preferences in female prairie voles (*Microtus ochrogaster*): a mechanism for pair bonding? *Behav Neurosci* 113:602–611.
- Williams SM, Goldman-Rakic PS. 1998. Widespread origin of the primate mesofrontal dopamine system. *Cereb Cortex* 8:321–345.
- Wise RA. 1996. Neurobiology of addiction. *Curr Opin Neurobiol* 6:243–251.
- Zald DH, Boileau I, El-Dearedy W, Gunn R, McGlone F, Dichter GS, Dagher. 2004. Dopamine transmission in the human striatum during monetary reward tasks. *J Neurosci* 24:4105–4112.
- Zink CF, Pagnoni G, Martin ME, Dhamala M, Berns GS. 2003. Human striatal response to salient nonrewarding stimuli. *J Neurosci* 23:8092–8097.